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# SYSTEMATIC PLACEMENT OF THE PLATANACEAE IN THE HAMAMELIDAE<sup>1</sup>

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## ABSTRACT

A cladistic analysis of the basal Hamamelidae based upon 92 characters is presented. The results support a close phylogenetic relationship between the subfamily Altingioideae (Hamamelidaceae) and Platanaceae but suggest that present hypotheses concerning the derivation of the Hamamelidae from the Magnoliidae need revision. Analysis of the five subfamilies of Hamamelidaceae using Platanaceae as an outgroup yields a phylogeny that corresponds to the fossil record far better than does current theory. As a result of this study and recent paleobotanical and phytochemical evidence, it is suggested that Hamamelidae are at least as primitive as Magnoliidae.

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Platanaceae are a monogeneric family of trees with a fossil history that extends to the Albian, Lower Cretaceous (Kutuzkina, 1974; Hickey & Doyle, 1977; Dilcher & Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwald, 1986). Cronquist (1981) considered Hamamelidales, which include Platanaceae, as an order of subclass Hamamelidae ancestral to all other orders within the subclass except the Trochodendrales. According to this view, Hamamelidales evolved from a Magnoliid or Magnoliid-derived taxon on a line of evolution that first spawned Trochodendrales. Recognition of Platanaceae as a well established angiosperm family in the Early Cretaceous raises questions concerning the current systematic placement of this family.

A diverse body of evidence supports a close systematic relationship between Platanaceae and Hamamelidaceae (Tippo, 1938; Jay, 1968; Takhtajan, 1969; Hickey & Wolfe, 1975; Cronquist, 1981; Zavada & Dilcher, 1986). Wolfe (1973) suggested a relationship between Platanaceae and Eupteleaceae based upon foliar characteristics.

Morphological similarities between Platanaceae and Hamamelidaceae—especially floral resemblances between hamamelidaceous subfamily Altingioideae and Platanaceae—strongly suggest alliance. However, there is no agreement concerning the relative advanced or primitive nature of the two families, and thus the extent of their relationship remains unresolved. Tippo (1938) felt that Platanaceae are “clearly more advanced than the Hamamelidaceae anatomically.” Cronquist (1981) considered Platanaceae to have been derived ear-

lier than Hamamelidaceae from a common stock of flowering plants. He commented that the flowers of Platanaceae are the more primitive of the two, but stated that “neither family can be derived from the other.”

## PROCEDURES AND METHODS

A cladistic analysis of the basal Hamamelidae—Eupteleaceae, Platanaceae, and the five subfamilies of Hamamelidaceae—was conducted using Swofford's PAUP (Phylogenetic Analysis Using Parsimony) program (Swofford, 1984) on Indiana University's mainframe computer. PAUP options were chosen to consider all possible trees on the basis of maximum parsimony. Character state polarities were established by outgroup analysis using Tetracentraceae and Trochodendraceae as outgroups.

Ninety-two characters are presented for each of the nine taxa in Table 1. Character states are coded for presence or absence for each of the nine taxa surveyed. Presence of a character state in any species of a given family or subfamily resulted in that taxon being scored as positive for the trait. The data used in our analysis were gleaned from the literature or generated by Schwarzwald (1986). The 92 characters include aspects of secondary chemical compounds, wood anatomy, epidermal characteristics, pollen structure, foliar morphology, petiole anatomy, seed structure, floral morphology and pollination adaptation, inflorescence type, and fruit type.

In our analysis the five subfamilies of the Hama-

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melidaceae, Altingioideae, Disanthoideae, Exbucklandioideae, Hamamelidoideae, and Rhodoleioideae, were treated as taxonomic equivalents to the Platanaceae, Eupteleaceae, Tetracentraceae, and Trochodendraceae. This subdivision was performed to insure a meaningful analysis of these taxa. The five subfamilies of the Hamamelidaceae are phenotypically quite distinct. Unlike the other families of the basal Hamamelidae, which display only minor genetic and phenotypic variation, the Hamamelidaceae, with 26 genera and more than 100 species (Cronquist, 1981), are extremely heterogeneous. If the family is analyzed as one taxon, the large degree of phenotypic variability encompassed by Hamamelidaceae tends to obscure intrafamilial and interfamilial relationships. Numerous authors have recognized the distinctness of the hamamelidaceous subfamilies and have recommended the elevation of one or more of them to familial status (Blume, 1928; Hayne, 1830; Lindley, 1836; Wilson, 1905; Nakai, 1943; Chang, 1959, 1964; Skvortsova, 1960; Willis, 1966; Takhtajan, 1969; Melikian, 1971, 1973a, b; Rao, 1974; Rao & Bhupal, 1974; Wolfe, 1973; Dahlgren, 1977; Jha, 1977).

These five subfamilies are considered as sister groups to Platanaceae and Eupteleaceae. Tetracentraceae and Trochodendraceae, together considered by Cronquist (1981) as members of the most primitive order within the Hamamelidae, were used as separate outgroups to establish character state polarities. Establishing character state polarities using the two families phenotypically closest to the Magnoliidae allows us to reconstruct Hamamelid evolution in relation to current evolutionary thought (Cronquist, 1981). By using Tetracentraceae and Trochodendraceae as outgroups we test the hypothesis of a Magnoliid-derived Hamamelidae. Cercidiphyllaceae and Myrothamnaceae are not considered in this analysis, because we feel that evidence suggests neither family as a hypothetical sister group to Platanaceae.

In order to determine the stability of relationships within the cladogram generated from this study, four test analyses were performed. In each test, 5% random error was introduced into the original data set, and PAUP was used to generate a cladogram(s). Using cladistics, one formulates the most direct course of evolution possible to hypothesize the evolutionary relationships of a given set of taxa. Evolutionary noise, i.e., homoplasy, occurs in a data set proportional to the extent that mosaic evolution occurs in a group of related taxa. Homoplasy is an expected component of any data set and tends to introduce ambiguity into cladistic re-

sults. The experimental addition of random error into this data set can be considered as extra homoplasy. Well-resolved relationships should be stable despite the addition of such evolutionary noise. Thus, this is a test of the stability of proposed relationships. Since cladistics formulates the evolutionary interrelationships of all taxa considered in an analysis, an error in the data set of one change in any taxon has ramifications for all taxa.

Rohlf & Sokal's (1981) statistical tables furnished random numbers. Three-digit random numbers were used to designate character states to be changed. The first digit of the number specified the taxon (1-9), and the last two digits specified the character (1-92). As all data are in presence-absence form rather than having three or more character states, characters could be reversed without ambiguity. Four tests of the initial cladogram (Fig. 1) were conducted. In each test 41 character states, 5% of the total 828 character states (92 characters for each of nine taxa), were reversed. A listing of the character states reversed in each of the four tests is presented in Table 2. Figure 2A-D illustrates the results of these tests. Consensus trees were calculated where more than one tree was determined to possess maximum parsimony. Swofford's CONTREE program, which uses the methods of Adams (1972) and Rohlf (1982), was used in these analyses.

## RESULTS AND DISCUSSION

The cladistic analysis resulted in one tree of a length of 157 steps (Fig. 1). In this cladogram, Platanaceae are placed within Hamamelidaceae sensu lato as a sister group to subfamily Altingioideae. Platanaceae and subfamily Altingioideae share 12 derived character states: the presence of cyanidin (character 5), glandular trichomes (character 17), actinodromous to palinactinodromous primary pattern of venation (character 42), the union of intercostal tertiary veins to secondaries (character 47), altingioid marginal venation (character 53), the presence of several vascular traces in petioles (characters 56 and 57), orthotropous ovules (character 60), small seeds (character 64), hard testas (character 69), minute petals (character 74), and nonperigynous flowers (character 83). The position of Eupteleaceae on the cladogram and the large synapomorphy list separating this family from Platanaceae and Hamamelidaceae suggest that Eupteleaceae and Platanaceae are more distantly related than is indicated by similarities of foliar features alone.

The cladogram suggests that Platanaceae orig-



TABLE 1. Continued.

	A	B	C	D	E	F	G	H	I
50. Teeth platanoid <sup>9,14</sup>	-	-	-	-	-	+	+	-	-
51. Secondary veins decurrent <sup>9,14</sup>	-	-	-	-	+	-	-	-	+
52. Teeth admedially oriented <sup>9,14</sup>	-	-	-	+	-	-	-	-	-
53. Altingioid marginal venation <sup>9</sup>	-	-	-	+	-	+	-	-	-
54. Teeth hamamelidoid <sup>9</sup>	-	-	+	-	-	-	-	-	-
55. Nodes unilacunar <sup>7,16</sup>	-	-	-	-	-	-	+	-	-
56. Number petiole traces = 1 <sup>7,16</sup>	+	+	+	-	+	-	-	+	+
57. Number petiole traces > 1 <sup>7,16</sup>	-	-	-	+	-	+	+	-	+
58. Petiole encloses axillary bud <sup>7,9,10</sup>	-	-	-	-	-	+	-	+	-
59. Stipules present <sup>7,17</sup>	+	+	+	+	+	+	-	+	-
60. Ovules anatropous <sup>16,18,19,20</sup>	+	+	+	-	+	-	+	+	+
61. Embryo narrow <sup>21</sup>	+	+	+	+	+	+	-	-	-
62. Raphe bundle enclosed <sup>18,21</sup>	-	-	-	-	-	-	-	+	+
63. Embryo minute <sup>16,18,21</sup>	-	-	-	-	-	-	+	+	+
64. Seeds small <sup>16,18,21</sup>	-	-	-	+	-	+	+	+	+
65. Subchalazal area vascularized <sup>16,18,21</sup>	-	-	-	-	-	-	-	+	+
66. Tegmen two-layered <sup>21</sup>	-	-	-	-	-	-	-	+	+
67. Tegmen persistent in mature seed <sup>21</sup>	+	+	+	+	+	-	-	+	+
68. Raphe bundle ending at chalaza <sup>18,21</sup>	+	+	+	+	+	+	-	-	-
69. Testa hard, conspicuous <sup>16,21</sup>	+	+	+	-	+	-	-	-	-
70. Carpels fused <sup>16,18,19,20</sup>	+	+	+	+	+	-	-	-	+
71. Carpel wall open <sup>16,18,19,20</sup>	-	-	-	-	-	+	-	+	+
72. Flowers imperfect <sup>16,18,19,20</sup>	-	+	+	+	-	+	-	-	-
73. Flowers perfect <sup>16,18,19,20</sup>	+	-	+	-	+	-	+	+	+
74. Petals minute or absent <sup>16,18,19,20,22</sup>	-	-	-	+	-	+	+	+	+
75. Sepals minute or absent <sup>16,18,19,20,22</sup>	-	+	-	+	-	+	+	-	+
76. Carpels sessile <sup>16,18,19,20</sup>	+	+	+	+	+	+	-	+	+
77. Stamens valvate <sup>16,17,18,19,20</sup>	-	-	+	-	-	-	-	-	-
78. Ovules > 1 <sup>16,17,19,20</sup>	-	-	+	-	-	+	-	-	-
79. Anemophilous <sup>16,17,18</sup>	-	+	+	+	-	+	+	+	+
80. Entomophilous <sup>16,17,18</sup>	+	-	+	-	+	-	+	-	+
81. Epigynous <sup>16,13,19,20,23</sup>	-	-	+	+	-	-	-	-	-
82. Hypogynous <sup>16,18,19,20,23</sup>	+	-	+	-	-	+	+	+	+
83. Perigynous <sup>16,18,19,20,23</sup>	-	+	+	-	+	-	-	-	-
84. Flowers solitary or in pairs <sup>16,17,18,19,20</sup>	+	-	+	-	-	-	+	-	-
85. Flowers in spikes <sup>16,17,18,19,20</sup>	-	-	+	-	-	-	-	+	-
86. Inflorescence a cyme or cymose raceme <sup>16,17,18,19,20</sup>	-	-	+	+	-	-	-	-	+
87. Flowers in heads <sup>16,17,18,19,20</sup>	-	+	+	+	-	+	-	-	-
88. Flowers in pseudanthia <sup>16,17,18,19,20,21</sup>	-	-	-	-	+	-	-	-	-
89. Fruit a follicle or follicetum <sup>16,17,18,19,20,21</sup>	-	-	-	-	-	-	-	+	+
90. Fruit capsular <sup>16,17,18,19,20,21</sup>	+	+	+	+	+	-	-	-	-
91. Fruit an achene <sup>16,17,18,19,20,21</sup>	-	-	-	-	-	+	-	-	-
92. Fruit a samara <sup>16,17,18,19,20,21</sup>	-	-	-	-	-	-	+	-	-

inated late in a series of evolutionary events that gave rise to the subfamilies of Hamamelidaceae. The position of Disanthoideae in the cladogram is corroborated by Cronquist (1968, 1981) and Takhtajan (1969); however, this is not unexpected since their placement of Disanthoideae is based upon their similarity to the Magnoliidae. However, the positions of Hamamelidoideae, Altingioideae, and Platanaceae as the most recently derived taxa of the group do not agree with the fossil record.

Members of the Platanaceae are first known from fossil leaves and reproductive material from the Albian, Lower Cretaceous (Kutuzkina, 1974; Hickey & Doyle, 1977; Dilcher & Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwalder, 1986). The first megafossil records of Altingioideae are leaves from the genus *Liquidambar* L. in the Cenomanian, lowermost Upper Cretaceous, (Newberry, 1898; Chesters et al., 1967) and Upper Cretaceous (Brown, 1933; En-

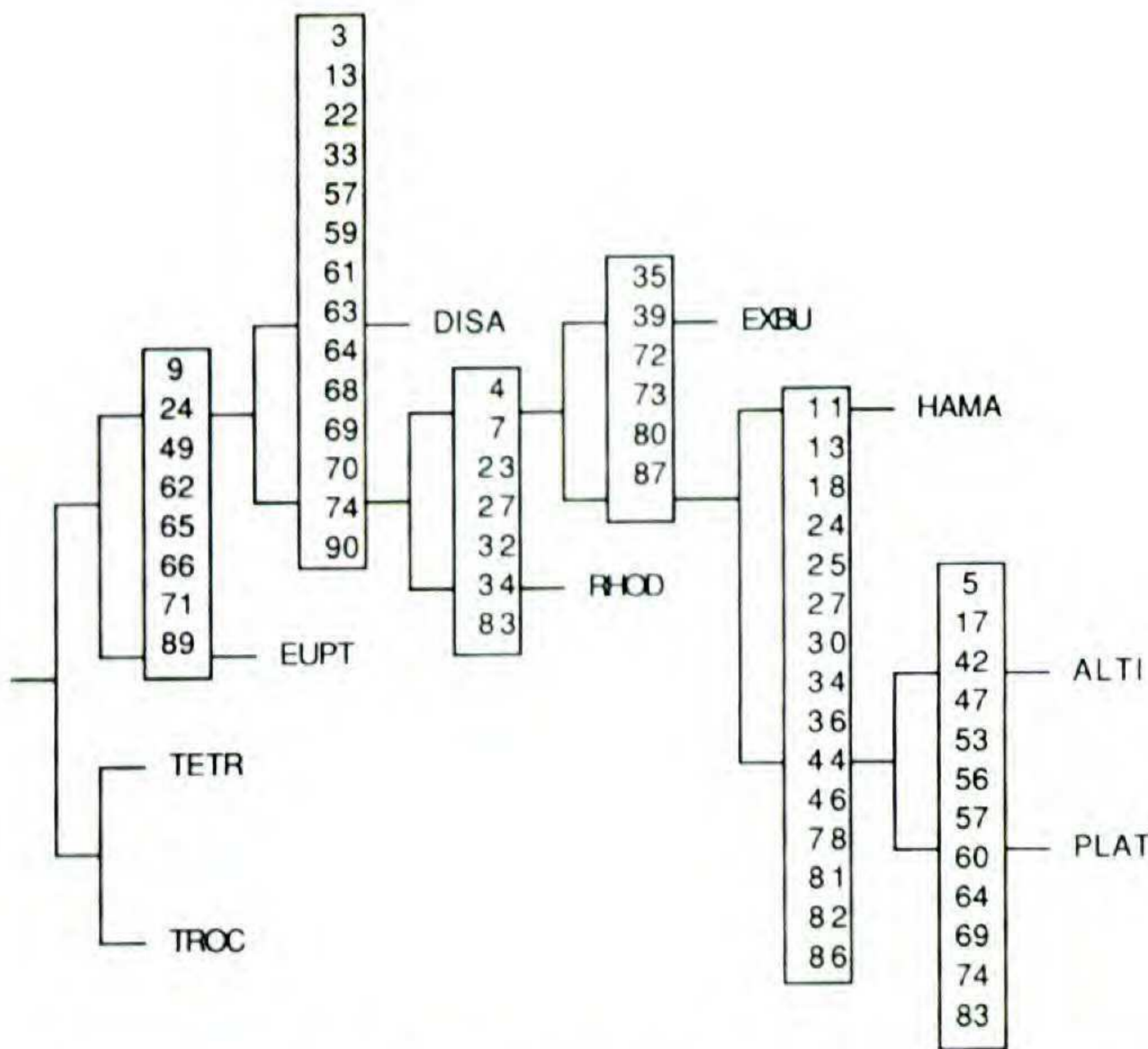


FIGURE 1. Cladogram of the basal Hamamelidae with Tetracentraceae and Trochodendraceae as outgroups. Synapomorphies are designated by rectangles. Numbers in rectangles make reference to character numbers in Table 1. Abbreviations above are as follows: TETR = Tetracentraceae, TROC = Trochodendraceae, EUPT = Eupteleaceae, DISA = Disanthoideae, RHOD = Rhodoleioideae, EXBU = Exbucklandioideae, HAMA = Hamamelidoideae, ALTI = Altingioideae, and PLAT = Platanaceae.

dress in Cronquist, 1981). The first records of megafossils from the Hamamelidoideae are foliar fossils from the lower Paleocene (Mathiesen, 1932; Hollick, 1936; Koch, 1963; Wolfe, 1966, 1973). The early fossil records of these putatively advanced taxa and the lack of early fossil representation of the other taxa in the cladogram suggest that the analysis may not be valid.

The discrepancy between these results and the fossil record prompted us to test the validity of our initial analysis. Four tests were performed by introducing 5% error into the data set and conducting cladistic analyses on each with the PAUP software. Results are presented in Figure 2.

The relationship between Altingioideae and Platanaceae, and the position of Eupteleaceae are preserved in the four consensus trees in Figure 2. The other subfamilies of Hamamelidaceae, however, are subject to extensive rearrangement with the addition of random error. Thus, the phylogenetic reconstruction of the basal Hamamelidae presented in Figure 1 is questionable if we assume that there is at least 5% homoplasy in the original data set.

A possible source of error in the hypothetical phylogeny presented in Figure 1 is the use of the two families of Trochodendrales as outgroups in the cladistic analysis. Fossil evidence of Platanaceae in the Albian, upper Lower Cretaceous (Kutzkina, 1974; Hickey & Doyle, 1977; Dilcher &

TABLE 2. Character state reversals for the tests of cladistic relationships in the basal Hamamelidae. Character state reversals are identified, by taxon, for each of the four tests presented in the body of the paper. Numbers given after each taxon correspond to the characters listed in Table 1.

Random Error Test One (Fig. 2A)	
Disanthoideae:	29, 33, 34, 54, 70, 89
Exbucklandioideae:	30, 38, 60, 80
Hamamelidoideae:	4, 14, 23, 27, 38, 57
Altingioideae:	68, 75
Rhodoleioideae:	2, 4, 23, 27, 31, 48, 52, 69, 82, 86
Platanaceae:	5, 76, 85
Eupteleaceae:	23, 56, 59, 64, 68, 71
Tetracentraceae:	59, 61, 76
Trochodendraceae:	65
Random Error Test Two (Fig. 2B)	
Disanthoideae:	30, 49, 71, 88
Exbucklandioideae:	25, 34
Hamamelidoideae:	23, 45, 52, 91
Altingioideae:	5, 15, 18, 20, 45, 51, 54, 86
Rhodoleioideae:	20
Platanaceae:	5, 59, 66, 78
Eupteleaceae:	16, 28, 43, 44, 46, 84, 89
Tetracentraceae:	18, 32, 42, 67, 73
Trochodendraceae:	1, 27, 40, 55, 64, 73
Random Error Test Three (Fig. 2C)	
Disanthoideae:	3, 31, 38, 59
Exbucklandioideae:	4, 19, 53
Hamamelidoideae:	18, 22, 34, 61, 77, 79
Altingioideae:	48, 52, 70, 80, 86, 91
Rhodoleioideae:	16, 18, 30, 43, 48, 52, 59, 76
Platanaceae:	5, 33, 52
Eupteleaceae:	32, 43, 66, 68
Tetracentraceae:	81, 91
Trochodendraceae:	19, 34, 56, 63, 69
Random Error Test Four (Fig. 2D)	
Disanthoideae:	7, 75, 77, 84, 87, 92
Exbucklandioideae:	4, 6, 39, 50
Hamamelidoideae:	3, 39, 78
Altingioideae:	10, 73, 88
Rhodoleioideae:	19, 58, 60, 65, 68, 71, 81
Platanaceae:	26, 28, 37, 62
Eupteleaceae:	23, 24, 54, 91
Tetracentraceae:	4, 12, 24, 25, 48, 66, 67, 81
Trochodendraceae:	40, 55

Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwaldner, 1986), predates the occurrence of any other member of the Hamamelidae. Hickey & Wolfe (1975) noted the early occurrence of the platanoids and suggested them as "possible early members of the trend toward the hamamelid line." If we assume that their early occurrence and morphological similarity to other members of

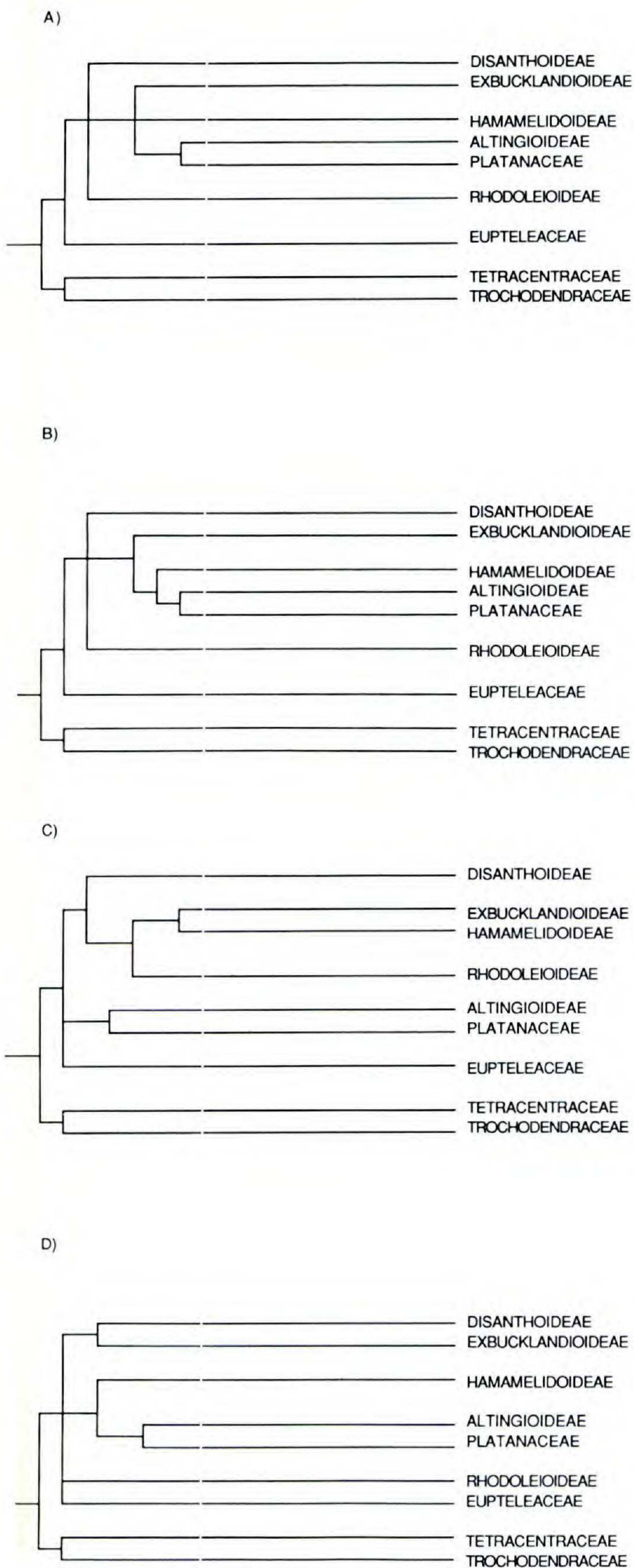


FIGURE 2. Adams consensus trees of the basal Hamamelidae with 5% randomly induced error; Tetracentraceae and Trochodendraceae are outgroups.—A. Consensus tree of three equally parsimonious trees (172 steps).—B. Consensus tree of two equally parsimonious trees (166 steps).—C. Consensus tree of three equally parsimonious trees (174 steps).—D. Consensus tree of four trees (174 steps).

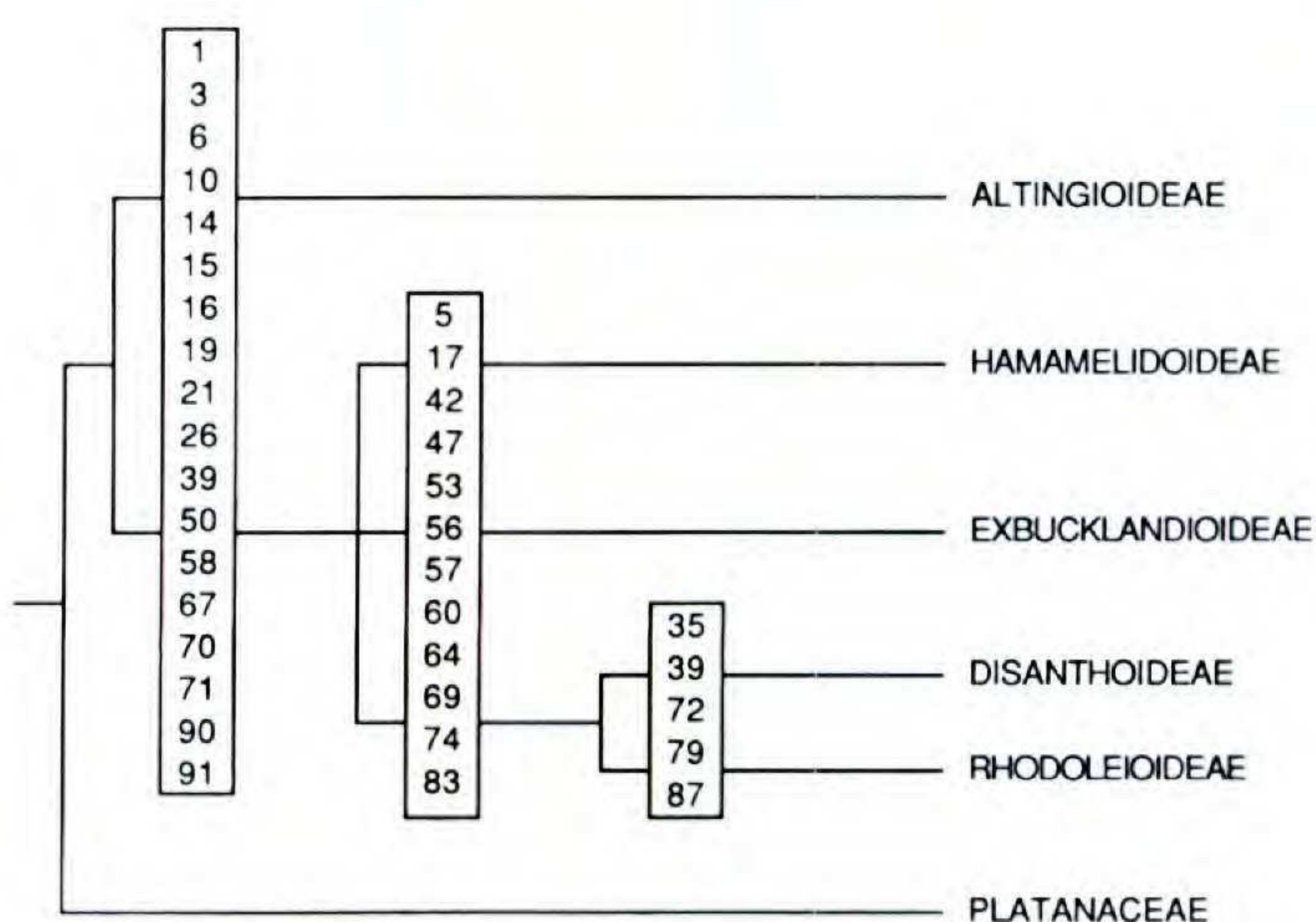


FIGURE 3. Adams consensus tree of two equally parsimonious trees where the Platanaceae serve as the outgroup. Synapomorphies are designated by rectangles. Numbers in rectangles refer to character numbers in Table 1.

the group demonstrate an early evolution from a hamamelid or prehamamelid lineage, and use the Platanaceae as an outgroup for analyzing the Hamamelidaceae, we obtain an alternative hypothesis of evolution in these two families (Fig. 3).

Figure 3 suggests that Altingioideae were the earliest-derived of the hamamelidaceous subfamilies. Later evolution in the family, according to the analysis, resulted in the evolution of the other four subfamilies with Disanthoideae and Rhodoleioideae being the latest-derived. While the consensus tree (Fig. 3) demonstrates the difficulty in resolving the node connecting Hamamelidoideae, Exbucklandioideae, and the Disanthoideae–Rhodoleioideae group, there is support for some of the relationships proposed by this cladogram. The position of Altingioideae as the earliest-derived subfamily of Hamamelidaceae is supported by 12 synapomorphies, which include features of phytochemistry, epidermal anatomy, venation, petiole anatomy, ovule and seed morphology, and floral structure (Fig. 3).

There is corroborative evidence from the fossil record for this phylogenetic scheme (Fig. 3). As mentioned previously, Platanaceae can be traced to the Lower Cretaceous, Altingioideae to the Upper Cretaceous, and Hamamelidoideae to the Lower Paleocene. Foliar megafossil records of Exbucklandioideae date from the Upper Oligocene (Lakhanpal, 1958) and Lower Miocene of Oregon (Brown, 1946) and the Middle Miocene of Washington State (Brown, 1946). We could find no records of fossil leaves, flowers, or fruits of the Disanthoideae or Rhodoleioideae. However, Tiffney (1986) reviewed records of dispersed seeds of *Rhodoleia* Champ. from the Upper Eocene (Mai & Walther, 1985) and *Disanthus* Maxim. from the

Lower Oligocene (Mai & Walther, 1978). These data suggest that Platanaceae may have been the earliest offshoot of a lineage that later gave rise to Altingioideae and, still later, Hamamelidoideae and other subfamilies of the Hamamelidaceae.

Hickey & Wolfe's (1975) suggestion that "Cercidiphyllales" and Trochodendrales form a clade separate from the remainder of the subclass that was derived from a prehamamelid or hamamelid lineage is in need of elaboration. Although our data suggest that the Eupteleaceae might be better placed in the Trochodendrales than the Hamamelidales, they lend some support for the derivation of the Hamamelidales from the "platanoids" proposed by Hickey & Wolfe (1975). The early occurrence of Platanaceae along with their cladistic proximity to Altingioideae and distance from Trochodendrales does not support inclusion of Trochodendrales in the lineage that led directly to the evolution of Platanaceae and Hamamelidaceae.

The cladistic analysis of the Hamamelidaceae using the Platanaceae as an outgroup results in a cladogram that differs drastically from current conceptions of evolution in the family (Cronquist 1968, 1981; Takhtajan, 1969) but agrees overall with the fossil record. We are not suggesting that this reconstruction represents the one true phylogeny of Platanaceae and Hamamelidaceae. Yet, we propose that the current practice of rooting the Hamamelidae in the Magnoliidae is in need of reevaluation. Paleobotanical (Dilcher, 1979; Retallack & Dilcher, 1981) and phytochemical data (Giannasi, 1986) suggest that Hamamelidae are at least as primitive as Magnoliidae. Examination of the Hamamelidae without assumptions as to their presumed ancestors may facilitate our understanding of the subclass and of angiosperm evolution.

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